

SPATIAL AND BEHAVIORAL FORAGING PATTERNS AND DIET SELECTIVITY
IN THE SOCIAL YELLOW BELLIED MARMOT

by

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Diss
1983
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Archives

Submitted to the Department of Systematics
and Ecology and the Faculty of the Graduate
School of the University of Kansas in partial
fulfillment of the requirements for the degree
of Doctor of Philosophy.

Dissertation Committee:

Chairman

Dissertation defended:
May 1982

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FORAGING PATTERNS OF YELLOW-BELLIED MARMOTS: ROLE OF KINSHIP
AND INDIVIDUAL VARIABILITY

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Summary

Two colonies of yellow-bellied marmots (Marmota flaviventris) at an elevation of 2900 m in Colorado were studied to elucidate the role of various behavioral and ecological factors as determinants of spatial foraging patterns. The locations of known individuals were periodically recorded. These locality data were plotted as three-dimensional block diagrams, the peak heights representing the frequency of observation. Predation risk and vegetation distribution influenced the location of foraging areas, but kinship was the most important factor in the determination of the amount of foraging area overlap between individual marmots. Overlap tended to be greatest among close kin, but this was modified by individual behavioral characteristics, reproductive state, the existence of separate burrow systems within a colony, and the age of the animal. Mothers and juveniles, and littermates as young and resident yearlings, had nearly identical foraging areas.

INTRODUCTION

A basic assumption of foraging theory is that fitness is enhanced by maximizing the efficiency with which an animal exploits its food resources. Efficiency usually is measured in terms of net rate of energy intake (Schoener 1971). As pointed out by Pyke et al. (1977), detailed knowledge of an animal's biology is necessary to determine how additional factors such as predation, nutritional requirements, or aggressive interactions influence foraging behavior.

An animal's decision regarding where to forage can be affected by an array of possible constraining factors. For example, the distribution of food resources might affect spatial patterns of foraging as animals feed extensively in areas rich in preferred food and spend less time where food is less desirable (e.g. blue geese, Harwood 1974; ungulates, McNaughton 1978). The way in which an animal uses space may be related to the space use patterns of its neighbors. A clumped distribution of individuals can result from, among other things, limited nesting sites or food resources. If animals live in close proximity, foraging areas must either be shared or be partitioned as a result of agonistic or avoidance behaviors.

The yellow-bellied marmot is an animal whose spatial patterns of foraging are affected by its burrow-dwelling habit and its membership in a social group. Marmots dig burrows in or near feeding areas (Armitage 1962), but predation risk could limit the distance at which an animal can safely forage. Social interactions could also determine where a marmot feeds. For example, to what degree are foraging areas shared among colony members? What effect does social status, relatedness, or individual behavioral characteristics have on spatial patterns? This

paper discusses the role of behavioral and ecological factors as determinants of spatial foraging patterns in these social animals.

MATERIALS AND METHODS

Yellow-bellied marmots (Marmota flaviventris) are large, semifossorial ground squirrels that are widely distributed in the western United States (Frase and Hoffmann 1980). Marmots in the study area emerge from hibernation in May, sometimes tunneling up through snow, and immerge in September after four to five months of activity. Courtship and mating occur in the first two weeks after emergence (Armitage 1965, Nee 1969). Gestation lasts about 30 days and the young remain in the burrow for another three to four weeks before emerging. A marmot in its first summer is termed a juvenile or young; a yearling marmot is in its second summer. All older animals are classified as adults. A typical colony consists of one or more territorial males, each with a harem of one to several females, sometimes yearlings, and young. Marmots may also live as single individuals, pairs, or in a mother-young group (Svendsen 1974). These herbivores eat a wide variety of grasses, flowers, forbs, and seeds (Svendsen 1973, Andersen 1975, Armitage 1979, Frase 1982).

Two colonies of yellow-bellied marmots were studied in the East River Valley, Gunnison County, Colorado at an elevation of 2900 m. Marmot Meadow (locality 4, Armitage 1974) is a meadow bordered by spruce-fir forest and dense willow thickets along the East River (Fig. 1a). The meadow includes several rocky outcrops, two of which contain home burrows. Picnic (locality 5, Armitage 1974) is a multi-harem site consisting of a talus area surrounded by meadow on a steeply angled slope (Fig. 1c). Several home burrows occur in the talus and rocky

outcrops. Only animals living at Lower Picnic, the area below the semicircle of spruce and aspen, were included in this study.

Data were taken from 25 June to 3 September, 1978; 24 June to 16 September, 1979; and 15 June to 3 September, 1980. Approximately 500 hours of observation were accumulated, more than half of these at Marmot Meadow. Lower Picnic data are from 1979 and 1980 only.

The marmots were live-trapped and permanently identified by numbered ear tags. Additionally each animal was marked dorsally with black fur dye in a unique pattern of blots or stripes to permit individual identification. (See Armitage 1962 for details on trapping and marking). Marmots were censused at ten minute intervals (15 minutes at Marmot Meadow in 1980 because there were too many animals to census in ten minutes) and the position of each marmot recorded from a clear numbered grid overlying a map of the area. Foraging activity also was noted at each census. Observation hours were concentrated in the morning and late afternoon when marmots are most active (Armitage 1962).

Social interactions were recorded; these behaviors can be classified as cohesive (= amicable, Armitage 1962, 1974) or agonistic. Allogrooming, play, and greetings are cohesive behaviors; agonistic behavior includes chases, fights, and avoidance. All forms of social interaction among marmots are most frequent in early summer (Armitage 1962, 1965, 1973).

A computer program (Surface II, Sampson 1975) plotted the census data as three-dimensional block diagrams, the peak heights representing the frequency of observation in each grid square (e.g. Fig. 2a). Plots of home ranges and foraging areas not included in this paper are compiled in Frase (1982). Averaging of peak heights within each plot

occurred to some degree. The only situation in which averaging resulted in significant changes in peak heights occurred when the frequency of observations in one grid square was much higher than in the others. The truncated peak was usually at the burrow entrance or a heavily used sunning/observation rock, where the observation frequency might be over five times the recorded number of observations at any other point in the study area. On plots representing foraging activity, the shortening of the highest peak was slight since there were no large differences in frequencies of observation among the grid squares. For example, in Fig. 4a, the maximum observed frequency in a grid square was 9; on the plot, this value was drawn as 7.89.

RESULTS

Social status and foraging area

Males. Adult male marmots are dominant to adult females (Armitage 1975). One male resided at Lower Picnic during the two summers of observation (Table I). Some of the colony members foraged in areas distinct from one another, but the foraging area of the resident male overlapped the areas in which other residents fed (Fig. 2a - 2d).

No males resided at Marmot Meadow in 1978 and 1979; in 1980, three males lived there for varying lengths of time (Table 1). Dominance relations among these males were complex and changing. Male 372 and ♂374 wrestled and chased each other, were observed to allogroom, and at times lay together at the entrance to Aspen Burrow. Male 519 chased ♂372; no interactions were observed between ♂519 and ♂374.

Male 374 moved into the locality on 16 June. During his first four days, he spent roughly equal amounts of time around Main Talus and Aspen Burrow. On 21 June, ♂372 entered the meadow and was immediately chased

by ♂374. However, ♂372 established residence at Aspen Burrow and foraged in that vicinity until he left in late July (Fig. 3d); the foraging activity of ♂374 was confined to the Main Talus area during this time (Fig. 3a). The third male, 519, appeared on 25 June. He first lived at Aspen Burrow, then moved into Main Talus (Fig. 3f). During ♂519's stay, ♂374 shared a foraging area around Aspen Burrow with ♂372 (Figs. 3b,3e). When ♂519 left Marmot Meadow 25 days later, ♂374 again concentrated his foraging around Main Talus (Fig. 3c).

Adult females. Dominant females sometimes spatially displaced other females. In 1978, two sisters living at Main Talus in Marmot Meadow (Table I) foraged in largely overlapping areas (Figs. 4a,4b). Although ♀911 was reproductive, no aggressive behaviors were observed between these females. The next year, reproductive ♀918 remained at Main Talus, but non-reproductive ♀911 moved to Aspen Burrow. Female 918 chased ♀911 whenever the latter approached to within a few meters of Main Talus. Female 911 was seen only sporadically after ♀110 moved into Aspen Burrow with her litter in early July (Table I) and was not observed anywhere in the meadow after 7 August. Although ♀918 inhabited a larger home range in 1979 than in 1978, her foraging again centered around Main Talus.

In 1980, three females, each with a litter, resided in the Meadow (Table I). Female ♀918 lived at Main Talus; ♀911 lived at Aspen Burrow until mid-June when she moved with her litter into Main Talus, despite initial agonistic behavior from ♀918. Female 179, the two-year old daughter of ♀911, lived at Spruce Burrow until early July when she and her litter moved to Main Talus.

All three females and their combined litters lived at Main Talus for the rest of the summer. Adult female foraging areas overlapped

extensively except that ♀179 fed in the northern extension of the meadow during the time she lived at Spruce Burrow (Figs. 4c,4d,4e).

At Lower Picnic also dominance relationships among females affected space use. In 1979, the foraging ranges of ♀1194 and ♀920 overlapped considerably (Figs. 2b,2c). Frequent cohesive behaviors were observed between these closely related marmots. The third female at Lower Picnic, non-reproductive 301, frequented the upper regions of the slope (Fig. 2d); her foraging area did not overlap that of the other females. Rare encounters with the other females resulted in ♀301 being chased.

In 1980, the same three females were present (Table I). The foraging area of non-reproductive ♀1194 encompassed the entire width of Lower Picnic. Reproductive ♀920 foraged in the same areas as in 1979 and added an area above and to the west of the talus. Female 920 also probably foraged further upslope; frequently she disappeared into the area while foraging, the tall vegetation there made observations difficult. Female 301 raised a litter at Spruce Burrow and her home range was again disjunct from those of the other females. The burrow itself was not visible from our observation post, and much of her activity occurred in areas not in view. There was no overlap of foraging areas between ♀301 and females 1194 and 920. Although foraging data were sparse for ♀301, the direction of trails leading from Spruce Burrow and occasional records indicate that her foraging was concentrated in the open meadow to the east of her burrow and downslope.

Yearlings. Yearling marmots are subordinate to adults, although all social interactions between them are not agonistic (Armitage 1975, Downhower and Armitage 1981). Yearling space-use patterns were affected by the behavior of adults toward them.

In 1979, at Marmot Meadow ♀918 chased her sister's yearlings. Observations of the three yearlings decreased as the summer advanced. By August, yearling appearance was sporadic; one individual was not seen at all in the latter part of the summer. Female 918 was aggressive toward her own yearlings in 1980. They roamed widely (Fig. 5a) and disappeared after 25 June. They did not occupy Aspen Burrow perhaps because four orphaned yearlings (Table I) remained there throughout the year. The foraging area of these Aspen Burrow yearlings did not overlap those of the Main Talus adults (Fig. 5b).

In 1979, the Picnic yearlings (Table I) frequented areas used by ♀301. These yearlings were raised as a common litter by ♀301 and her sister who disappeared in late summer of 1978. Space-use patterns of all three 1980 yearlings were similar; a typical yearling foraging area overlapped those of ♀1194 and ♀920 (Fig. 5c).

Young. At least one litter of young lived at Marmot Meadow each year of the study. In 1978 and 1979, the Main Talus young fed in the same area as their mother (e.g. Fig. 4b,5d). In 1979, a weaned litter was brought from outside the meadow to Aspen Burrow by ♀110 (Table I). Four days after their arrival, this adult female was killed. Her orphaned young remained at Aspen Burrow and foraged mostly in the eastern section of the meadow. The areas of most intensive use by this orphaned litter were disjunct from those areas most used by ♀918's litter, although individuals from both litters did feed in the meadow between the two burrow systems. Although ♀918 did visit Aspen Burrow, she did not molest any orphan. No evidence of fostering behavior by ♀911 was observed.

The foraging area of the three litters at Main Talus in 1980 (Table I) was more extensive than that of any previous litter in this study, and included the meadow above Main Talus and to the north, an area little used in other years (Figs. 6a-6c). Foraging was more frequent in that area than our figures indicate. The tall vegetation and uneven topography made it impossible to census every young. The heavy use of these areas was indicated by a newly-created marmot trail leading northward from Main Talus and by the observation of young entering that area only to "disappear" for several censuses and to reappear at some visible point nearby. There were only a few excursions to the Aspen Burrow area.

The four young at Picnic in 1979 fed in much the same areas as their mother. As with the litters occupying separate burrow systems in Marmot Meadow, there was little overlap between the areas frequented by the two Picnic litters in 1980.

Seasonal changes in foraging area.

At Marmot Meadow, the newly emerged juveniles stayed close to the burrow site. Subsequently, they gradually enlarged their home range and added to their foraging area. For example, in 1980, during the first two weeks after emergence, the young moved only as far as the rocks just west of Main Talus (Fig. 6a). During the second two weeks, they expanded their usage of the meadow considerably (Fig. 6b). There was little change in their range in the next two weeks, except for the addition of a fairly distant foraging area to the north (Fig. 6c).

Picnic young did not exhibit quite the same pattern. Due to the topography of the site, foraging is not possible in the immediate vicinity of most home burrows, and thus these young animals move to

fairly distant points to feed soon after emergence. The areas in which they foraged changed little as the summer progressed.

The emergence of the young had negligible effect on the spatial foraging patterns of other resident marmots. Commonly, there were no material differences between the mothers' foraging areas pre- and post-emergence of a litter although the post-emergence foraging areas of the mothers appear to be larger than during pre-emergence in most cases (Frase 1982). This difference, in part, results from the greater number of locality records from the usually longer post-emergence interval. Importantly, however, there is no marked shift in space usage that would segregate the feeding areas of a female from her litter. Occasionally, definite, within-summer changes in the space use patterns of a yearling were temporally correlated with young emergence (Frase 1982). Because such spatial changes did not occur universally among the sibship or within one sex, the cause of the changes probably was not emergence of a litter.

DISCUSSION

Foraging area and competition for food

Reproduction in female marmots may be food limited to varying degrees (Andersen et al. 1976). For such animals, food availability is particularly important in the first weeks after emergence from hibernation. For all marmots, sufficient food resources are necessary for adequate fat deposition prior to hibernation. Overwinter survival of young in particular is strongly affected by their ability to gain at least a minimum weight by immergence (Armitage and Downhower 1974, Armitage et al. 1976). If food were a limited resource, marmots should exhibit some form of competitive behavior.

By foraging in a different area than her young, a mother marmot might minimize food competition between herself and her litter. She could forage further from the burrow to allow her offspring adequate forage nearer to safety. However, mothers and young have similar foraging areas and a mother's relative use of near-burrow foraging areas does not decrease after her litter emerges.

A female might attempt to obtain exclusive use of a foraging area (as do some female hoary marmots, Barash 1974) to ensure sufficient forage for herself and her young. Of the nine females with litters observed during this study, only two had exclusive foraging areas. The isolation of ♀301 at Picnic in 1980 was not self-imposed, but resulted from intolerance by the other resident females. By contrast, highly aggressive ♀918 at Marmot Meadow in 1979 shared a foraging area only with her litter and actively excluded other marmots from her home range. In a marmot population consisting of several contiguous harems, exclusive use of forage areas was only 10% for individual animals (Johns and Armitage 1980). All of the above indicate that competition for food is not responsible for the foraging patterns observed in yellow-bellied marmots. Indeed, marmot population density is probably not restricted by food abundance (Kilgore and Armitage 1978); marmots consume only 0.9 to 3.1% of the aboveground primary production in a year. However, because marmots forage selectively (Armitage 1979, Frase 1982), vegetative distribution might affect the spatial foraging patterns.

Vegetational distribution

The vegetation in Marmot Meadow is characteristic of a Festuca thurberi grassland community (Langenheim 1955). Dominant species included the grasses Bromus richardsonii and Stipa lettermani,

cinquefoil (Potentilla gracilis), and dandelion (Taraxacum officinale) (Kilgore 1972, Frase 1982). The vegetation was distributed fairly uniformly and was of low diversity. Grasses, cinquefoil, and dandelion ranked highest in importance value (IV) (Svendsen 1973). Together, these three constituted 88.9% of the summed IV's for Marmot Meadow's herbaceous vegetation.

Choice of foraging areas by marmots at Marmot Meadow probably was not affected by plant distribution to any great degree. In 1980 it was noticed in late summer that the vegetation for several meters around Main Talus was unusually sparse and short. A zone of biodeterioration around a central refuge is not uncommon (Hamilton and Watt 1970), and in this instance was no doubt due to the combined effects of trampling and foraging by 22 marmots, perhaps exacerbated by an exceptionally dry summer. Animals continued to forage around the burrow, but it was at this time that the young began to utilize the area to the northwest (Fig. 6c).

Picnic vegetation was more diverse and clumped. Large, showy perennials such as columbine (Aquilegia caerulea) and fireweed (Epilobium angustifolium) were abundant. Grasses, cinquefoil, columbine and fireweed had the highest IV's, constituting 75% of the summed IV's of the herbaceous vegetation.

At Picnic, marmots were observed to cross the slope to feed in an area particularly rich in a preferred plant species (Frase 1982). Picnic animals occasionally foraged in the talus on ripe raspberries or columbine flowers growing between the rocks. In an alpine area, the only parts of the basin not within the foraging area of some individual were those in which Geum rossi, a plant not utilized by marmots, was

abundant (Andersen et al. 1976). Plant distribution and marmot selectivity therefore, can influence spatial foraging patterns, although these factors apparently are relatively minor in determining where an individual feeds. Vegetation patterns may restrict foraging to within certain areas, but because marmots do not forage in all vegetationally suitable places, other factors must be responsible for an individual's spatial foraging pattern.

Location of refugia

The intensity of predation on a forager may affect the distance it can travel from a refugium (Covich 1976). Predation on marmots seldom has been observed (Frase and Hoffmann 1980, Armitage 1982) and there is no good measure of the strength of predation pressure as a selecting factor. Marmots may forage long distances from their burrow. At Marmot Meadow, the young frequently fed over 40 meters from the nearest burrow. Typically, the distance between a foraging marmot and any burrow was less than 20 m. At Picnic, home burrows were in the talus where little foraging was possible. There are, however, upwards of 70 burrows in the colony area (Svendsen 1974); consequently, a marmot usually was not far from a refuge. In most cases, a foraging animal responding to an alarm call by a colony member, runs from the outlying meadow toward its home burrow, or at least to the talus to sit alertly on a rock. If danger were imminent, these animals would take refuge in the closest burrow and not run all the way to the talus. Foraging does tend to occur in areas close to a home burrow (e.g. Marmot Meadow) or another refuge burrow; other factors being equal, predation risk probably precludes foraging further afield.

Space sharing and kin selection

Marmot colonies may be largely occupied by matriarchal lineages of females. Sixty-one per cent of the females resident in socially stable colonies in the East River Valley were living in their natal colony (Schwartz and Armitage 1980). Thus, some harem-mates are closely related. In an alpine population of yellow-bellied marmots, a higher rate of cohesive behavior was observed among closely related animals than among relatively unrelated individuals (Johns and Armitage 1979). Most marmots do not maintain exclusive use of either foraging areas or burrow (Armitage 1965, 1975, Johns and Armitage 1979, this study), but knowing the degree of relatedness between individuals might allow us to predict with whom these resources are most likely to be shared.

All young born to colony residents remain with their mother at least through the first winter; many disperse the following year (Armitage and Downhower 1974). A female and her litter occupy the same burrow which may be shared with other marmots. In Olympic (M. olympus) and hoary (M. caligata) marmots, a parous female and her litter maintain exclusive use of a burrow; other adults and yearlings may live together (Barash 1973, 1974). Burrows are not shared among adult European marmots, M. marmota (Barash 1976).

In yellow-bellied marmots, mothers and young have similar home ranges as expected. Kinship, however, is only a partial predictor of the amount of space sharing among other individuals, although closely related adults did share space.

Aggressiveness may increase in reproductive female marmots (M. flaviventris, Armitage 1962, 1965, Downhower 1968; M. monax, Bronson 1964; M. caligata, Barash 1974), and this heightened aggressiveness may

explain ♀918's intolerance of her non-reproductive sister. Her intolerance was not due to a lack of adequate resources at Main Talus to support herself, her litter and her sister, since in other years, two or three adults and three to fifteen young lived at Main Talus without conflict (Table I). Female 918's failure to exclude her sister and her niece in 1980 may be due to the increased aggressiveness of these now reproductive females. The agonistic encounters between ♀918 and the dominant adult males that appeared may have reduced ♀918's general level of aggressiveness at the time the other two females with litters were attempting to move into the better burrow system. (It appears that the Main Talus burrow system is superior to the Aspen Burrow system. In nineteen years of observation at this site, when only one of the two areas was inhabited, it was always Main Talus, and in other years, yearlings or subordinate adults lived at Aspen Burrow). On the other hand, ♀1194 and ♀920 shared space at Picnic regardless of their respective reproductive conditions. However, even when reproductive, ♀301 did not attempt to move into a burrow occupied by another female; her use of space did not overlap with the other females, whether she had a litter or not. She was more distantly related to ♀1194 and ♀920 than the latter two were to each other (Table I) and she had shared a burrow with her sister prior to 1979.

The relative shortness of this study, compared to the number of reproductive years of a female marmot, does not allow determination of whether sharing space with kin enhances inclusive fitness. Thus far, by not being tolerant of kin, ♀918 appears to be faring poorly regarding her contribution to the gene pool. None of her daughters were recruited into the colony, and while achieving no clear competitive advantage, she

engaged in activities which could have decreased the fitness of her sister and niece and their offspring. Female 911 on the other hand, had a daughter reproduce as a resident two-year old. Possibly ♀918 attempted to increase her individual fitness by excluding other adult females. That she failed does not preclude the success of this strategy under other circumstances and enable a female to obtain exclusive use of resources for herself and her offspring. This strategy might be expected when a female is reproductive. Although her yearlings may disperse, she will be more closely related to her offspring than to her grandchildren. This strategy was predicted from the model of marmot polygamy (Dowhower and Armitage 1971), but subsequent studies indicate that the individual strategies of marmots are more complex (Armitage 1975, 1977, Armitage and Johns 1982). However, retaining her offspring in their natal area until they are yearlings increases the probability of their reproducing and thus increases a female's fitness (Armitage and Dowhower 1974). More information is needed on the fate of dispersers to determine when dispersive or recruitment strategies are successful.

Patterns of space use might affect the amount of aggression among marmots in such a way that proximity rather than relatedness becomes an important determinant of which animals coexist in a colony. For example, ♀918 may have tolerated the orphans but not her own yearlings because the former lived at Aspen Burrow while the latter did not have any similarly distant burrow system to occupy. Aspen Burrow could serve as a "refuge" for individual marmots not tolerated by Main Talus residents. In 1979, ♀911 was chased by ♀918 only when ♀911 approached Main Talus closely; she was not harassed in the vicinity of Aspen Burrow. At Picnic, the relative infrequency of agonism between ♀301 and females 1194 and 920 probably resulted from their spatial separation.

Kinship, then, is an important factor in the determination of the amount of foraging area overlap between individuals. In a large alpine population of marmots, exclusive use of foraging areas among burrow groups (on the average closely related to each other) was 41%; exclusive use increased to 88% if all harem members (degree of relatedness much less than among burrowmates) were considered (Johns and Armitage 1979). In this study, space sharing tended to be greatest among close kin, but this pattern was modified by individual behavioral differences and the existence of separate burrow systems within a colony site. The only consistent patterns are forage area sharing between a mother and her young and the nearly identical patterns of space usage within a litter, as young or as resident yearlings.

Acknowledgments This work is part of a dissertation submitted by B. Frase in partial fulfillment of the requirements for the Ph.D. degree at the University of Kansas. Field research was funded by NSF Grants DEB 78-07327 and DEB 81-21231 and was conducted at the Rocky Mountain Biological Laboratory, Colorado. We thank R. S. Hoffmann and R. Jander for critically reading the manuscript. The Kansas Geological Survey generously allowed the use of their plotting facilities; we are grateful to M. Sharifi and G. Aspiazu for doing many of the plots. Computer funds were provided by the University of Kansas.

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Figure 1. Photographs and Surface II-generated plots of the study sites showing home burrow locations. M Main Talus; A , Aspen Burrow; S Spruce Burrow; L Slope Burrow; R, Split Rock. Grid squares at Marmot Meadow are 3m square, those at Picnic are 9m^{x5m} square.

- a. Marmot Meadow from the west
- b. Marmot Meadow plot
- c. Picnic from the south
- d. Picnic plot

Figure 2. Surface II-generated, three-dimensional plots of space use patterns of adult yellow-bellied marmots at Picnic, 1979.

- a. ♂125; foraging area
- b. ♀1194; foraging area
- c. ♀920; foraging area
- d. ♀301; home range

Figure 3. Surface II-generated, three-dimensional plots of foraging areas of three adult males at Marmot Meadow, 1980. Space usage changed during the summer, correlated with the changes in male residency. Period 3: 21 June-23 June, Period 4: 25 June-16 July, Period 5: 18 July-31 August.

- a. ♂374; period 3
- b. ♂374; period 4
- c. ♂374,, period 5
- d. ♂372; period 3
- e. ♂372; period 4
- f. ♂519; period 4

Figure 4. Surface II-generated, three-dimensional plots of foraging area use by adult yellow-bellied marmots at Marmot Meadow.

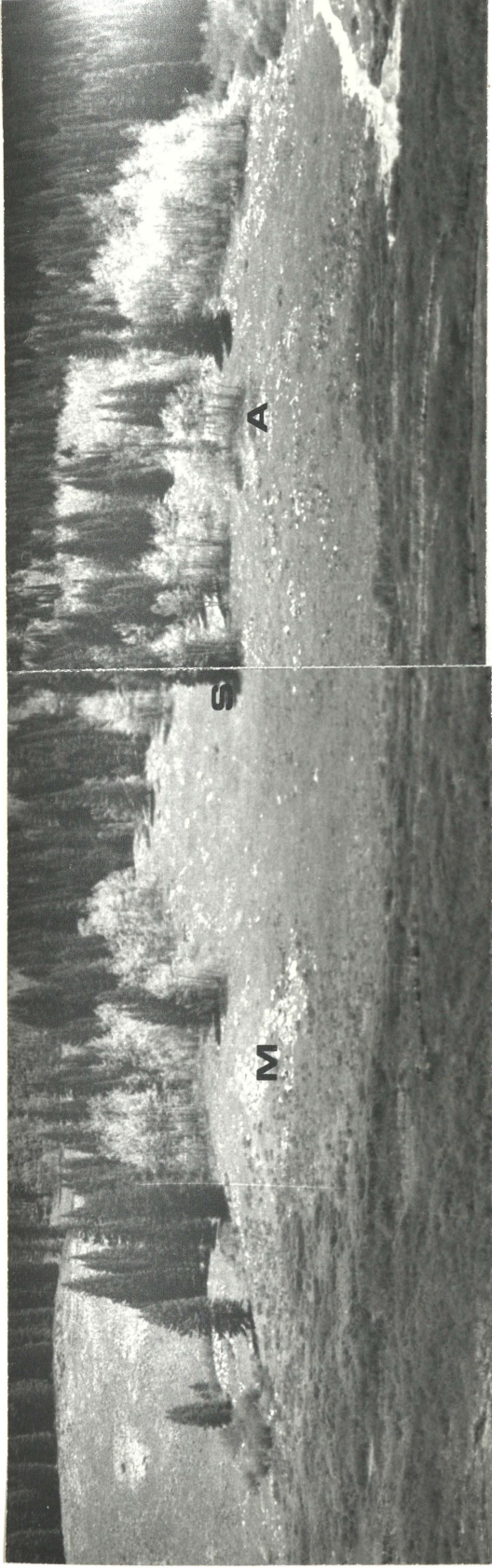
- a. ♀918, 1978
- b. ♀911, 1978
- c. ♀918, 1980
- d. ♀911, 1980
- e. ♀179, 1980

Figure 5. Surface II-generated, three-dimensional plots of space use patterns of yearling and young yellow-bellied marmots.

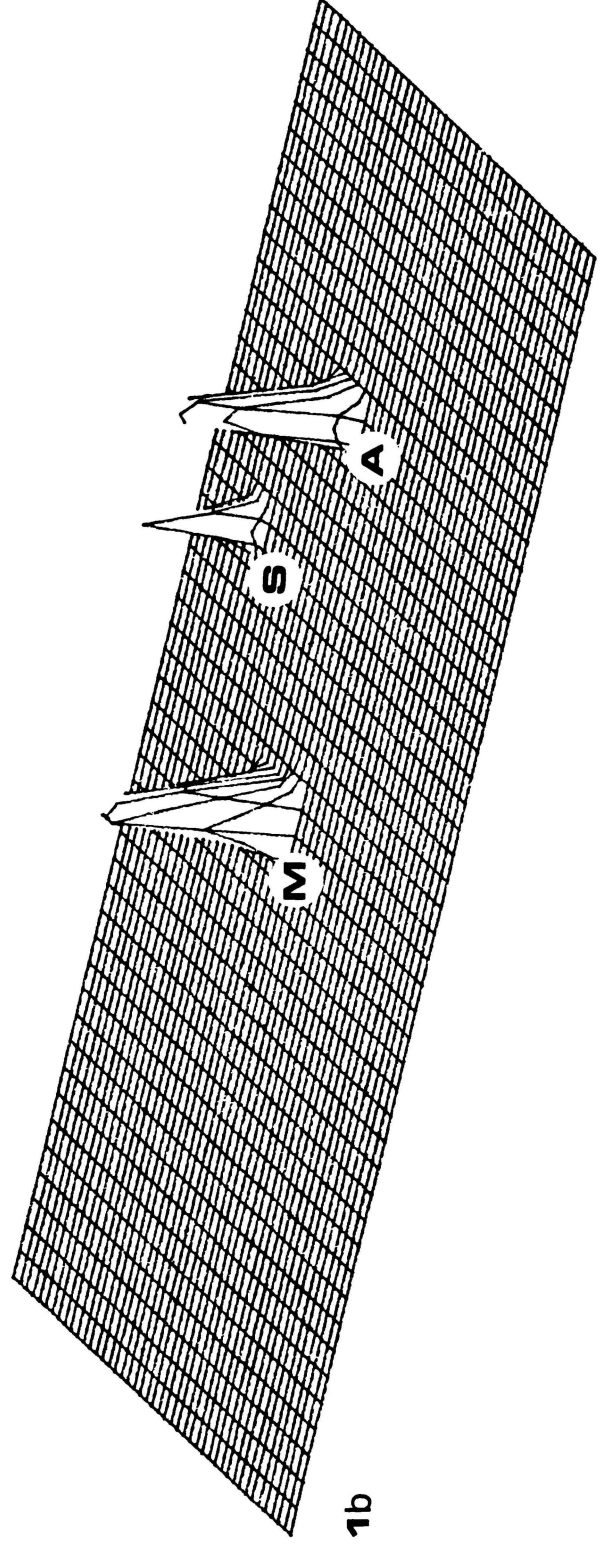
- a. Main Talus yearlings combined home ranges, 1980
- b. Typical orphaned yearling foraging area, 1980
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Figure 6. Surface II-generated, three-dimensional plots of temporal changes in combined foraging areas of Main Talus young and their mother, ♀918, 1980.

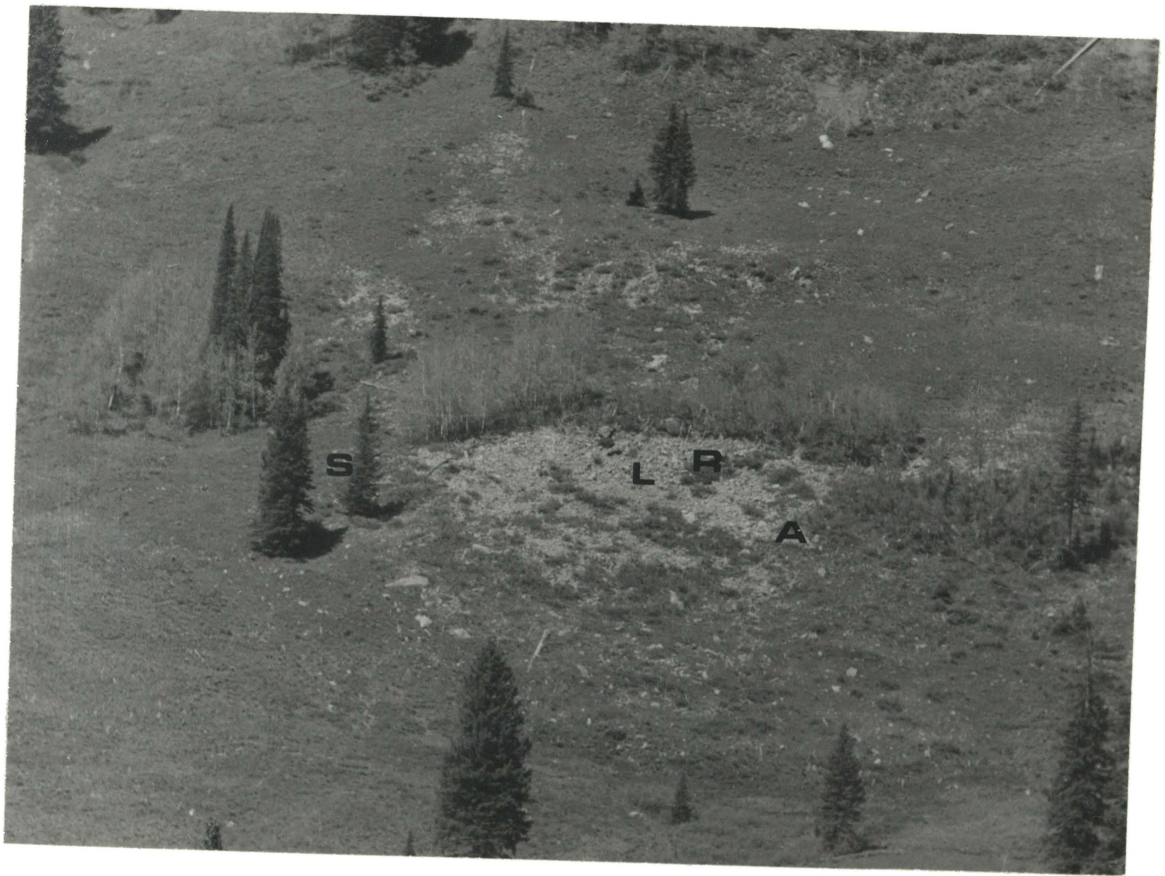
- a. Young: first two weeks post-emergence
- b. Young: second two weeks post-emergence
- c. Young: third two weeks post-emergence



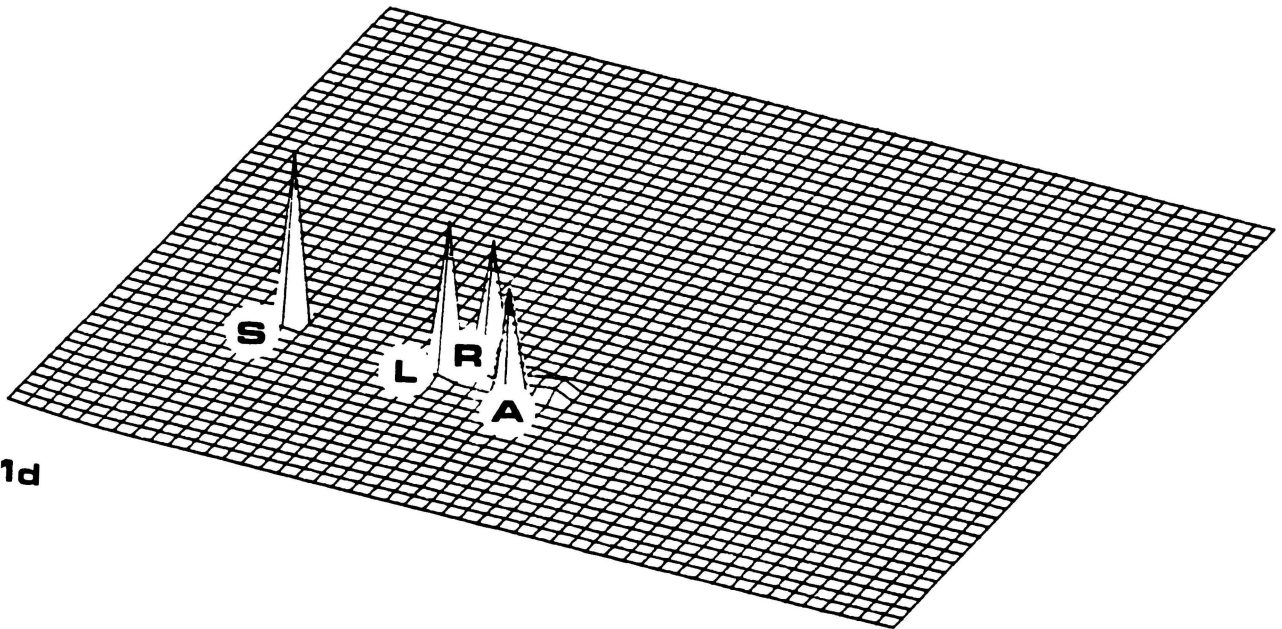
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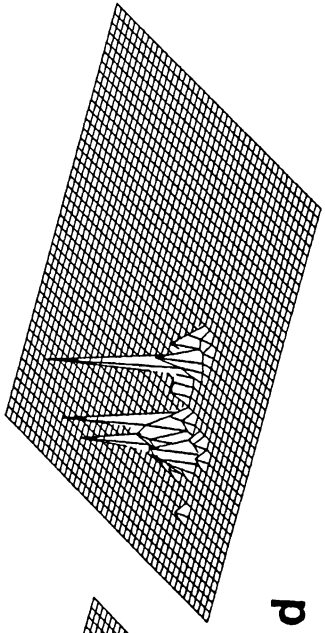
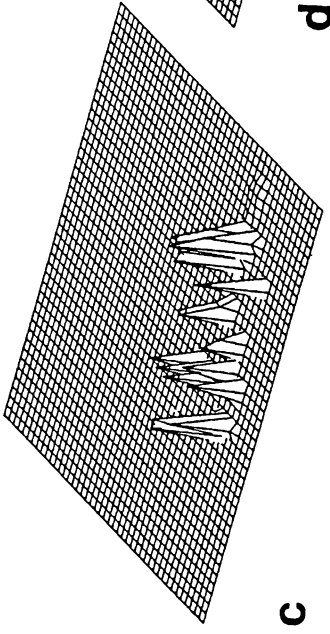
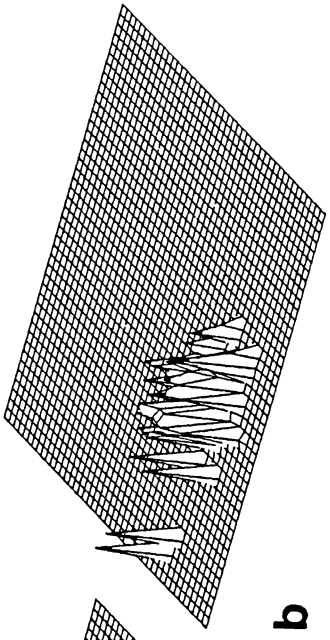
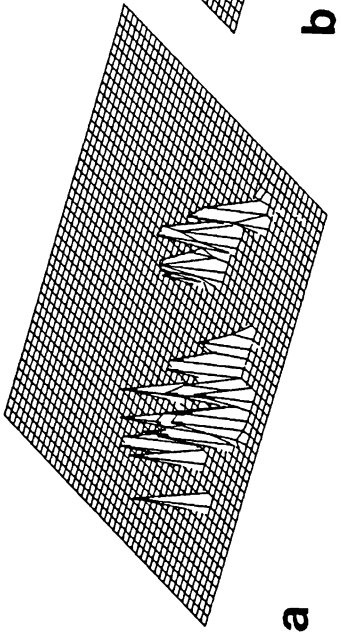
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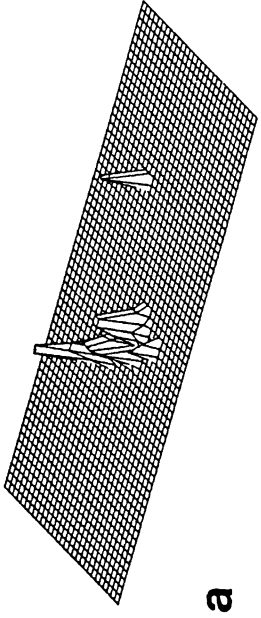


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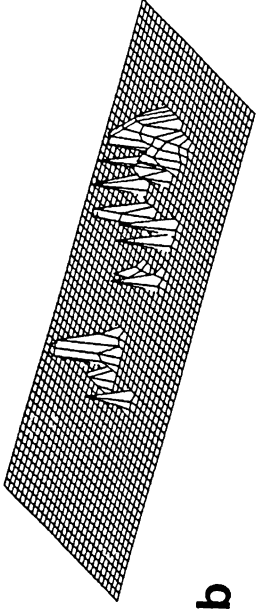


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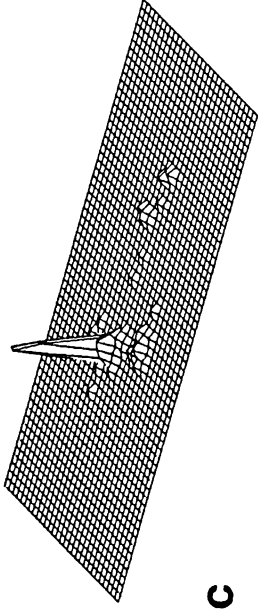




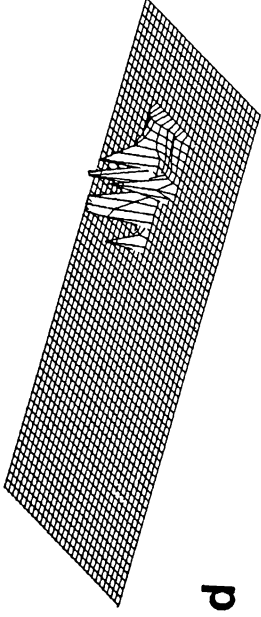
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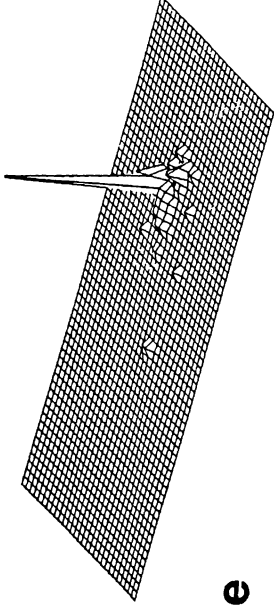
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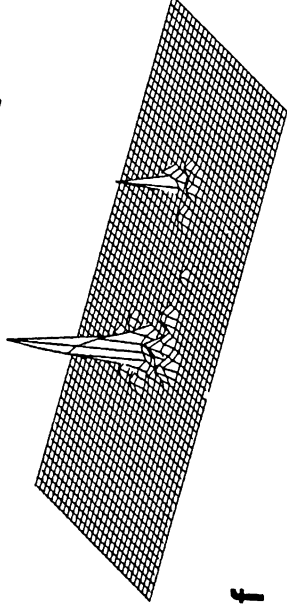
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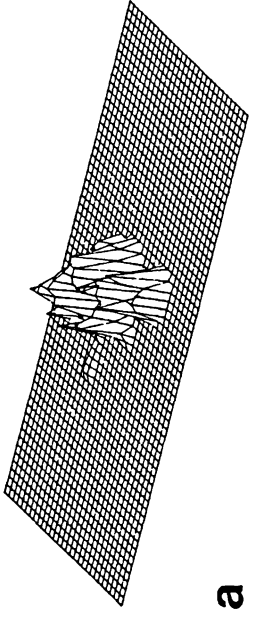
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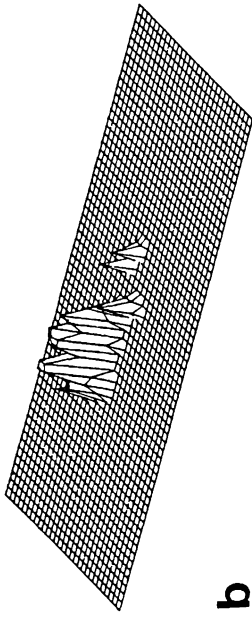
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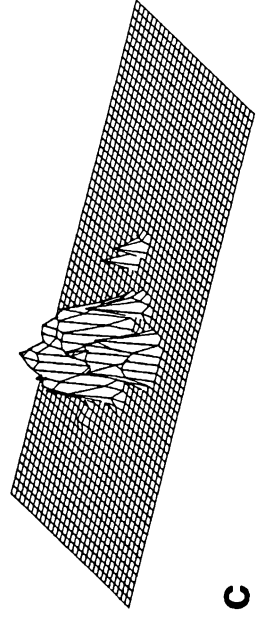
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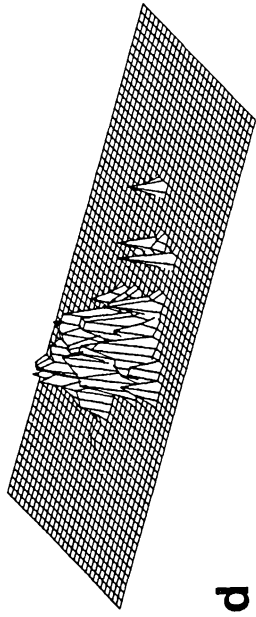
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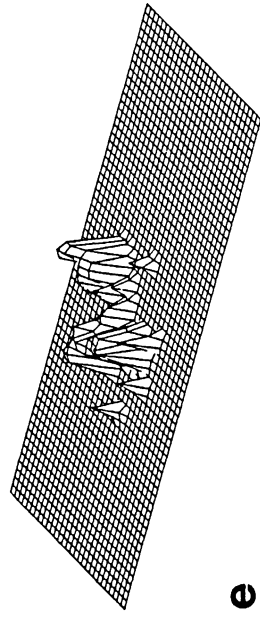
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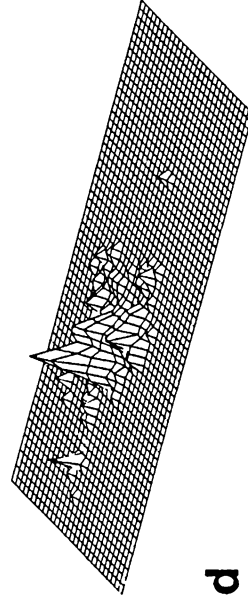
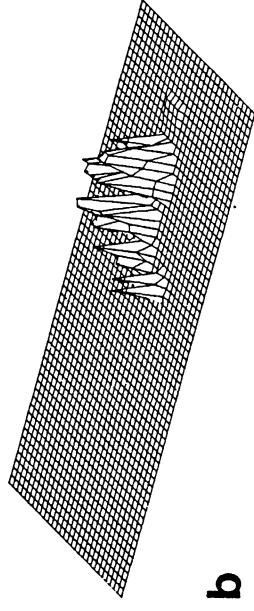
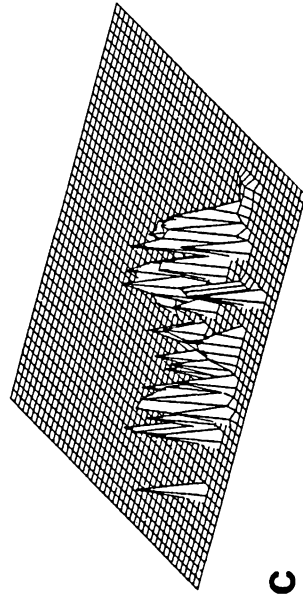
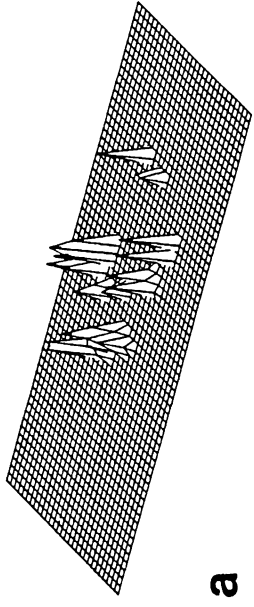
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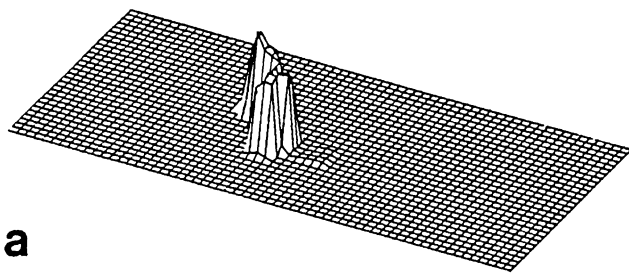


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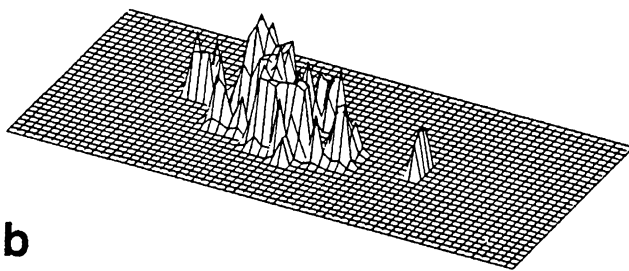


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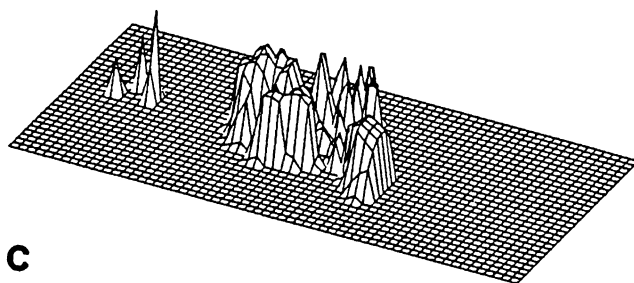




a



b



c

Table I. Population structure and home burrow use. Litter size in parentheses. Parentheses enclosing individual marmot numbers indicate a short-term use of the burrow. Burrow locations shown in Fig. 1a-1d. denotes reproductive female.

MARMOT MEADOW				
	<u>Main Talus</u>	<u>Aspen Burrow</u>	PICNIC	
			<u>Split Rock</u>	<u>Spruce Burrow</u> <u>Slope Burrow</u>
1978	2 yr. old sisters ♀911*(4) ♀918			
1979	(♀911) ♀918*(3)	(♀110*, died) litter (7) ♀911	♀301, 5 yr. old ♂125, second yr. of residency Yearlings young of ♀301 or sister	
1980	♀911* ♀918* ♀179*, 2 yr. old daughter of ♀911 Combined litters (15) ♂374, adult (♂519, adult)	Yearling orphans (♂372, adult)	♀1194	♀301*(6) ♀920*(4) ♂125

TIME BUDGETS AND FORAGING BEHAVIOR
OF THE YELLOW-BELLIED MARMOT

BARBARA A. FRASE

ABSTRACT

A colony of yellow-bellied marmots (Marmota flaviventris) in Colorado at an elevation of 2900 m was studied to determine temporal patterns of foraging of individuals throughout their active season. The percentage of aboveground time spent foraging for each animal was obtained by instantaneous scan samples at 10 min intervals. The percentage of time spent foraging varied widely among individuals. As a group, adults and yearlings allotted a significantly lesser proportion of time to foraging activity after mid-July. The absolute amount of foraging time decreased later in the summer, although the proportion of time did not. Juvenile marmots nearly doubled the percentage of time engaged in foraging in late summer. The time budget of one adult female was calculated from eighty-nine, 5 min continuous behavioral samples. This female spent more than 70% of her aboveground time sitting or lying in an alert position. Foraging occupied less than one-third of her time, and social interactions accounted for less than 1%. Emergence of her litter did not affect her time budget.

INTRODUCTION

An important aspect of the ecology of any animal is the way in which it apportions time among different activities. Time budgets are shaped by, among others, activities that must occur at a particular time, place, or context (Altmann 1974). These activities might be scheduled on an annual (e.g. reproduction or hibernation) or on a daily (e.g. return to burrow to avoid thermal stress in mid-day) basis. It is predicted, therefore, that behavioral budgets will exhibit seasonal changes (Bekoff and Wells 1981), related either to changes in the requirements of the animal (e.g. increased energy input to support lactation, resulting in more time spent foraging), or changes in the environment (Maxton and Oring 1980), (e.g. a decrease in quantity of food resulting in an increase in search time).

Time budgets of yellow-bellied marmots (Marmota flaviventris) were investigated to determine whether the proportions of time devoted to various behaviors differed among individuals and over time. For example, do all age/sex classes of marmots spend the same amount of time foraging? How does the emergence of a litter affect the time budget of a reproductive female? Does the proportion of time allocated to foraging change as the vegetational characteristics change and the time of hibernation approaches?

Basic Marmot Biology

Yellow-bellied marmots are large, semifossorial ground squirrels that are widely distributed in the western United States (Frase and Hoffmann 1980). Marmots in the study area in the East River Valley emerge from hibernation in May, sometimes tunneling up through snow. They are active only four to five months and immerge in September.

Courtship and mating occur in the first two weeks after emergence (Armitage 1965, Nee 1969). Gestation lasts about 30 days and the young remain in the burrow for another three to four weeks before emerging. A marmot in its first summer is termed a juvenile or young; a yearling marmot is in its second summer. All older animals are classified as adults. A typical colony consists of one or more territorial males, each with a harem of one to several adult females, sometimes yearlings, and young. Marmots may also live as single individuals, pairs, or in a mother-young group (Svendsen 1974). These animals are herbivorous and eat a wide variety of grasses, flowers, forbs, and seeds (Svendsen 1973, Andersen 1975, Armitage 1979, Frase and Armitage 1983a).

MATERIALS AND METHODS

Data were collected by observing a colony of marmots in the East River Valley in western Colorado at an elevation of 2900 m. Marmot Meadow (locality 4, Armitage 1974) is a meadow bordered by spruce-fir forest and dense willow thickets along the East River. The meadow includes several rocky outcrops, two of which contain home burrows.

Field studies were conducted from 25 June to 2 September in 1978, from 24 June to 16 September, 1979, and from 15 June to 3 September, 1980. Marmots were observed with a Quester field model telescope for approximately 300 hours. Observation was concentrated in the morning and late afternoon during the animals' peak activity times (Armitage 1962).

The animals were live-trapped early in the spring, and small metal numbered ear tags were affixed for permanent identification. Each marmot was marked dorsally with black fur dye in a unique pattern of blots or

stripes to permit individual identification during observations (see Armitage 1962 for details on trapping and marking). Marmots were censused at ten minute intervals (15 minutes in 1980 because there were too many animals to census in ten minutes). Foraging activity of each individual was recorded at each census.

The proportion of time spent foraging based on the census data was calculated for three periods during the summer; 1) the four weeks prior to emergence of a litter in the colony; 2) the first four weeks after litter emergence; and 3) the remaining days of the study (16 days in 1978, 6 days in 1979, 11 days in 1980).

Continuous five-minute behavioral samples were recorded in the field on a custom-built microprocessor-based data recorder. Eight behavioral categories were distinguished: 1) Feed - feeding on vegetation with head down; 2) Up-alert - front paws raised off substrate; 3) Locomote - walk or run without simultaneous foraging behavior; 4) Alert - head raised while feeding or head at a level higher than dorsum while sitting or lying; 5) Groom - autogrooming; 6) Interact - any cohesive or agonistic behavior, including greeting, allogrooming, chasing; 7) Sit/lie - resting posture. A sitting animal was simultaneously alert (behavior 4); a lying animal may or may not have been alert, but in reality, the time spent lying in a non-alert posture was trivial; 8) Other - rare behaviors other than those listed, including digging, gathering grasses, etc. Only behaviors 4 and 7 could occur simultaneously. Foraging activity comprised alternating feeding and alert behavior.

Each behavioral category was assigned a key on the keyboard of the data recorder. During the five-minute observations, the appropriate key

was depressed for the duration of each behavior. The resultant information was stored as sequences of behavioral acts (key presses) and the amount of time (in tenths of seconds) since the beginning of the sampling period that each key was pressed or released. After each sampling period these data were read from the microprocessor memory onto a cassette tape. At the end of the field season, the cassette tapes were read back through the microprocessor directly into the KU Honeywell 66/60 computer and stored on tape. These data provided information on the frequency and duration of each behavioral state.

All statistical tests are from Sokal and Rohlf (1969).

RESULTS

Because the number of censuses varied among animals and among time periods, the foraging records obtained from censusing could simply reflect the number of censuses, i.e. the more censuses of an animal, the higher the proportion of foraging records. To test for a correlation between these variables, the proportion of foraging records was regressed on the number of censuses, calculated for each animal for each two week period. The regression indicated that differences in numbers of censuses did not bias the data ($r = 0$, $p > 0.2$ and $\beta = 0$, $p > 0.05$).

The time spent foraging ranged widely among individual marmots and among the three time periods (Table I). For all classes of individuals for which we have data the proportions of time spent foraging in 1978 were much lower than in either 1979 or 1980. The values among animals in one class within one year were as variable as values among one class between years. In 1980, one female yearling significantly decreased her proportion of foraging time between period 1 and period 2, another

foraged a significantly lower portion of time in period 3 than in period 2, and a third displayed no significant differences throughout the entire season (Table I). The seasonal pattern of foraging time of reproductive females was not consistent for any female for two years, or between two females within one year. Per cent of time foraging of the adult male was generally high. One striking pattern was the near doubling of the per cent of time foraging of the young between period 2 and period 3 in 1979 and 1980.

To determine whether there was a population trend despite individual variation, the means of the proportions for all adults and yearlings in each time period were compared with the t-statistic (Table I). The means for periods 1 and 2 were not statistically different but the t-value was close to the critical value and the difference between the means may be biologically significant. The means for periods 2 and 3 were equal. The difference between the means for all reproductive females in period 1 and 2 was close to significant, and the means for female yearlings were significantly different in period 1 and 2. Thus, despite differences among individuals, there was a pattern of decreased foraging activity, usually beginning in late July.

Eighty-nine five-minute behavior samples were accumulated on reproductive female 918 in 1979. The mean per cent of time spent foraging based on these data was 25.9 (Table II); this agreed closely with the mean of the census data, 31.1 (Table I). More than 70% of all time was spent sitting or lying in an alert or up-alert position. Foraging occupied less than 30% of the active period of the day; social interactions accounted for less than 1% of the activity.

The time budget of this female prior to emergence of her young, was compared to that following emergence. There were no significant differences in any behaviors (Chi-square test of independence, 0.05 level of significance) pre- and post-emergence. A Chi-square test of the frequency of up-alert behavior indicated no change between the two time periods. A female thus does not change her alert behavior when the young emerge; her alert times does not increase nor does she alert more frequently but for shorter periods of time.

Foraging consists of sequences of feeding and alert behavior. The mean duration of feeding episodes during each 5 minute sample ranged from 2 to 11 seconds. Alert behavior means were typically less than 3 seconds. Head-down times were variable, but the alert time was evidently just long enough for a marmot to scan the area.

DISCUSSION

The single most time-consuming activity of the marmots was resting. Travis and Armitage (1972) also reported that sitting occupied the majority of the marmot's time from 0630 to 0900 MST. Kilgore's (1972) observations over 24-hour periods demonstrated that resting was the prevalent behavior. This pattern is surprisingly common and many endothermic animals spend the bulk of their awake time inactive (Herbers 1981). Herbers suggested that this inactive time represented a buffer that allowed an animal to increase the time involved in foraging activities during times of food stress. Yellow-bellied marmots do not need such a buffer. They are not food-limited (Andersen et al. 1976, Frase and Armitage 1983b) and they spend less time foraging in spring and late summer when food quantity or food quality are most likely to be

limited (Frase and Armitage 1983a), than in mid-season (Johns and Armitage 1979, this study). Herbers used the term laziness to describe inactivity for which there was no demonstrated ecological or physiological function. Laziness may not describe resting in marmots; sitting or lying on rocks may have an important thermoregulatory function in marmots and might not be time "left over" after other needs (e.g. obtaining food) have been satisfied. Basking in free-living Abert's squirrels (Sciurus aberti) resulted in an elevated body temperature and was an important component of thermoregulatory behavior (Golightly and Ohmart 1978). Time is required for digestion of food; perhaps in marmots, food processing as well as thermoregulation occurs during rest.

Because we have field data on only one non-reproductive female, and individual variation is so great, it is difficult to determine the effect of gestation and lactation on a female's forage requirements. We would expect that reproductive females would have greater nutritional needs and forage longer than non-reproductives. Indeed, of 918's three summers, she foraged the least the year she had no litter, and the foraging means for all reproductive females were greater than the values for non-reproductive 918 in all periods (Table I).

The juvenile marmots dramatically increased the proportion of foraging time after their first month above ground in 1979 and 1980. Juveniles in a colony in Yellowstone National Park, Wyoming (Armitage 1962) nearly doubled the proportion of time spent foraging in the second four weeks post-emergence compared to the first four weeks post emergence in 1956 and 1957 (Armitage, unpublished data). Young marmots lose about 50% of their total body weight during hibernation (Armitage

et al. 1976) and it is therefore crucial that they obtain a threshold weight by fall. Blaxter (1968) implied that juvenile animals, in contrast to adults, must increase food intake to gain weight. Body size of young marmots increases during their first month aboveground, and the later increase in foraging might be necessary to achieve prehibernation fattening as well as continued growth. Juvenile Belding's ground squirrels (Spermophilus beldingi) hibernate at the age of 3 months, roughly the same age as young marmots. The ground squirrels gained weight throughout the summer, but with a plateau in mid-season followed by a rapid gain (Morton et al. 1974). This pattern is interpreted as a shift from general growth to lipogenesis, because significant quantities of lipid were deposited only after mid-August. We would predict the same pattern in juvenile marmots. The protein content of forage plants decreases as the summer advances (Frase and Armitage 1983a); perhaps an increase in foraging time also was required to obtain sufficient protein for growth, either because more vegetation was eaten or because the marmot spent more time selecting more protein-rich plant parts.

Interestingly, several other changes occurred in young marmots after their first month aboveground. Home ranges were established and underwent little further expansion (Frase and Armitage 1983b), blood characteristics were "adult-like" (Armitage 1982), and juveniles responded to mirror image stimulation (Svendsen and Armitage 1973) instead of huddling in a corner of the arena as they did previously. All these events imply that some maturational processes were completed at this time and perhaps associated physiological changes were related to the pattern of increased foraging.

Hibernation is one of the scheduled events (Altmann 1974) that greatly affect marmot time budgets. Yellow-bellied marmots and other species of hibernating ground squirrels have a circannual cycle of food consumption (Davis 1967; Ward and Armitage 1981). In marmots maintained in the laboratory for 2 years, food consumption decreased by 50% during August and September, while at the same time body weight increased. A reduced metabolic rate allowed the weight gain despite the decrease in food intake.

Thus it was expected that the percentage of time spent foraging by non-juveniles in the field would decrease in late August and September as hibernation approached. Foraging in hoary marmots (Marmota caligata) (Barash 1976) and in an alpine population of yellow-bellied marmots (Johns and Armitage 1979) decreased late in the season. Although in this study, only some animals reduced the proportion of time foraging, the population as a whole foraged less after mid-July. Observations ceased before the animals hibernated; another sharp decrease in foraging probably would have occurred prior to immergence. It is important to note that most marmots spend less time aboveground in late summer in our study area (Kilgore 1972, personal observation). Therefore, although the proportions of time spent foraging were not significantly less for all animals, the absolute amount of time spent foraging decreased during the last sampling period. As predicted by laboratory studies, the wild non-juvenile marmots were able to deposit sufficient fat for hibernation while actually decreasing foraging activity late in the season.

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Acknowledgments. This work is part of a dissertation submitted by B. Frase in partial fulfillment of the requirements for the Ph.D. degree at the University of Kansas. Field research was funded by NSF Grants DEB 78-07327 and DEB 81-21231, and was conducted at the Rocky Mountain Biological Laboratory, Colorado. We were especially grateful to Wes White who designed and built the microprocessor data recorder. We thank R.S. Hoffmann and R. Jander for critically reading the manuscript. Computer funds were provided by the University of Kansas.

TABLE I. Proportion of aboveground time spent foraging. Period 1 -four weeks prior to emergence of a litter in the colony. Period 2 -first four weeks post-emergence of a litter. Period 3 - "pre-hibernation". Means compared with t-test, differences between proportions tested with Chi-square tests of independence. * significant at the 0.05 level. R - reproductive female, (N) after young each year - number of young in a colony. Means are underlined.

	1	<u>Period</u> 2	3	<u>p values</u>	
				1 vs 2	2 vs 3
Adult females					
R♀911 (1978)	14.1	14.9	11.6	>0.05	>0.30
R♀911 (1980)	35.0	26.7	15.0	>0.10	0.1>p>0.05
R♀918 (1979)	34.5	25.5	33.3	0.1>p>0.05	>0.20
R♀918 (1980)	34.0	19.0	13.7	<0.01*	<0.30
R mean	<u>29.4</u>	<u>21.5</u>	<u>18.4</u>	0.1>p>0.05	>0.05
♀918 (1978)	20.4	18.0	10.0	>0.50	≅-0.05*
Adult ♂374 (1980)	38.7	38.8	28.3	>0.80	<0.01*
Yearling ♂479 (1980)	25.0	24.0	41.5	>0.80	<0.05*
Yearling females (1980)					
♀458	32.4	14.2	10.6	<0.01*	>0.30
♀469	31.8	20.0	26.3	0.1>p>0.05	>0.30
♀479	25.5	24.5	19.6	>0.80	>0.50
mean	<u>29.9</u>	<u>19.6</u>	<u>18.8</u>	<0.05*	<0.80
Adults and yearlings (\bar{X})	<u>29.1</u>	<u>21.6</u>	<u>21.0</u>	0.1>p>0.05	>0.05
Young					
1978 (4)		13.8	17.4		>0.20
1979 (3)		16.4	34.9		<0.01*
1980 (16)		15.0	30.5		<0.01*
mean		<u>15.1</u>	<u>27.6</u>		<0.01*

TABLE II. Proportion of aboveground time spent in various behaviors, based on 5-minute continuous samples of reproductive female 918 in 1979. Foraging = feeding + (alert - sit/lie). Proportions sum to more than 100% because sit/lie and alert can occur simultaneously.

	<u>Foraging</u>	<u>Feeding</u>	<u>Up-alert</u>	<u>Locomote</u>	<u>Alert</u>	<u>Sit/lie</u>	<u>Groom</u>	<u>Interact</u>	<u>Other</u>
Pre-emergence of									
young (n=32)	29.0	19.1	10.2	3.7	62.0	53.5	1.3	0.4	0.3
Post-emergence of									
young (n=57)	28.8	20.1	8.5	2.1	68.9	60.2	1.1	1.1	0.1

THE INFLUENCE OF NUTRITIONAL CHARACTERISTICS OF VEGETATION
ON THE DIET OF THE YELLOW-BELLIED MARMOT

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ABSTRACT

The basis on which a mammalian herbivore selects forage species is complex. Yellow-bellied marmots (Marmota flaviventris) eat a wide variety of grasses, forbs and seeds, but do not feed on all items in proportion to their abundance in the environment. In this study, correlations between the marmot diet and crude protein, water caloric value, relative biomass and toxicity of the available plant species were investigated. The epidermis of all forb species does not survive digestive processes equally well; therefore, a complete quantitative analysis of the animals' diet based on fecal sampling was precluded. However, it was apparent that marmots did not choose their food plants on the basis of any one factor examined.

Why do animals eat what they do? Recent investigations of diets of mammalian herbivores have focussed on the relative importance of various plant properties such as protein content, secondary compounds, caloric value, mineral content, etc., to an animal that forages selectively (Batzli and Sobaski, 1980; Milton, 1980; Owen-Smith and Novellie, 1982). The relationship between various nutritional properties and palatability is not consistent for all animals (Westoby, 1974) and can vary seasonally within one species (Goldberg et al., 1980). Obviously, the basis on which food is chosen is complex, and models that consider only one factor are probably not realistic.

Yellow-bellied marmots (Marmota flaviventris) are generalist herbivores that eat a variety of grasses, flowers, forbs, and seeds (Svendsen, 1973; Andersen, 1975; Armitage, 1979). Marmots feed selectively, however, and in the laboratory rejected plants known to contain secondary compounds (Armitage, 1979). Nutrient constraints and the relative abundance of plant species also may influence selectivity, and it is of interest to determine how the marmot diet is correlated with various plant characteristics. In this study, data were obtained on crude protein, water content, caloric value, and the relative biomass of vegetation in colony sites of the yellow-bellied marmot in Colorado.

METHODS

Yellow-bellied marmots are large semi-fossorial ground squirrels that are widely distributed in the western United States (Frase and Hoffmann, 1980). Marmots in the study area emerged from hibernation in May, sometimes tunneling up through snow. A typical colony consists of one or more territorial males, each with a harem of one to several adult females, usually yearlings, and young.

Vegetation was analyzed at two colony sites near the Rocky Mountain Biological Laboratory at Gothic, Colorado at an elevation of 2900 m. Marmot Meadow (locality 4, Armitage, 1974) is a meadow bordered by spruce-fir forest and dense willow thickets along the East River. The vegetation on Marmot Meadow is characteristic of a Festuca thurberi grassland community (Langenheim, 1955). Dominant species included the grasses Bromus richardsonii and Stipa lettermani, cinquefoil (Potentilla gracilis), and dandelion (Taraxacum officinale) (Kilgore, 1972). The vegetation was distributed fairly uniformly and was of low diversity (Frase and Armitage, 1982).

Picnic (locality 5, Armitage, 1974) is a site consisting of a talus area surrounded by meadow on a steeply angled slope. Picnic vegetation was more diverse and clumped (Frase and Armitage, 1982). Large, showy perennials such as columbine (Aquilegia caerulea) and fireweed (Epilobium angustifolium) were common.

Between 26 June and 11 September 1979, and 23 June and 21 August 1980, grasses and herbaceous vegetation were sampled at

Marmot Meadow and Picnic at approximately two week intervals. A grid system and a random numbers table were used to choose sampling points at Marmot Meadow. Twenty-two 10 x 25 cm quadrats were clipped to within 1 cm of the ground; at Picnic, the vegetation in ten 10 x 25 cm randomly placed quadrats on each of three 50 m transect lines was clipped. The plants were separated by species, dried, and weighed to the nearest 0.1 g. All grasses were combined.

For each collecting day the plants were grouped into one of three categories, high relative biomass, medium relative biomass, or low relative biomass. Species contributing more than 20% to the total biomass were placed in the high category, those contributing less than 10% were in the low category (Table 1).

The nitrogen content of the plants collected in 1980 from clipped quadrats was determined with a Coleman Model 20A Nitrogen Analyzer. Care was taken to include tissue from more than one individual plant in each analyzed sample, and only completely unfurled and green leaves and stems were included. To varify that there was little variation in N-content among individual plants at one location on each sampling day, analyses were performed on two subsamples of Potentilla gracilis from each of the five sampling days. The nitrogen analyzer is accurate to within $\pm 0.3\%$; the results from the paired subsamples were within this range, indicating that intra-individual variation in N content was trivial.

For each sampling period, species wre placed in a high, medium, or low crude protein group. The groups were determined

by dividing the number of species among the three categories as equally as possible, while maintaining species with equivalent crude protein (within 0.3% of each other) in the same group. In the last sampling period, there were no natural divisions; when ranked, the crude protein value of each species was equivalent to the value of the next in rank. Arbitrarily, the two species highest in rank were considered high in crude protein, the next two medium, and the last three low (Table 2).

Water content was determined by subtracting the dry weight of several individual plants of each species from the wet weight. The difference divided by the wet weight was expressed as the percent water content. Species with a water content greater than 80% were considered high in water, those with water content below 70% were placed in the low group (Table 3).

Ten forbs plus grasses and a sedge were ranked according to caloric value (Kilgore, 1972); the highest ranking four species were placed in the high caloric group, the next four in the medium caloric group, and the lowest ranking four in the low caloric group (Table 4).

Fecal pellets were collected on vegetation sampling days. These pellets were prepared for microhistological examination following the technique of Hansen (1971). Samples were oven-dried and individually ground in a Wiley mill over a 1 mm screen. A subsample was mixed with boiling water in a blender for 30 sec, drained, and placed in bleach for 30-60 sec to initiate clearing. Each bleached sample was washed over a 200 mesh screen and mounted directly into Hoyer's solution on a

slide. The same method was used to make reference slides of fourteen forbs growing in the colony sites (grasses were combined), except that the ground plant samples were placed directly into bleach. Epidermal characteristics of each forb and the grasses were determined from these reference slides; mixtures of species were made to verify that individual species could be discriminated. Twenty fields from each fecal sample were examined microscopically, and the presence or absence of each plant species noted. A field was counted if there were at least two recognizable fragments in it. Grasses were not identified to species.

Frequency percentages derived from the fecal pellets were converted to relative density (Fracker and Brischle, 1944), and the relative density of a species was used to determine the percentage dry weight of the species in the diet (Sparks and Malechek, 1968).

Epidermal fragments of grasses and sedges were easily distinguished from those of forbs. Grasses and Carex have rectangular cells with undulating walls in a linear arrangement; forb epidermal cells are irregular in shape and randomly arranged (Howard and Samuel, 1979). Among the forbs, Vicia and Lathyrus were difficult to distinguish and were combined into one category. Mertensia fusiformis and M. ciliata were histologically similar. Because their phenology differed (M. fusiformis appeared early in the season and was not present later in the summer), the date of fecal collection was used to decide which Mertensia was present.

Accurate quantification of forbs in the diet using fecal analysis is possible only if the epidermis of all species survives digestion (and sample preparation) equally well. Some workers reported that all epidermis does not survive digestion (Slater and Jones, 1971; Anthony and Smith, 1974). The extent to which the relative numbers of forb fragments accurately reflect diet composition may depend on the digestive processes of the animal being studied as well as the "delicacy" of the forbs' epidermis.

Several captive yearling marmots were fed diets of fresh vegetation of known species composition in order to obtain fecal material from known diets and to determine whether any species were rejected. Animals were fed 100 g of either a single species or a mixture in the morning and late afternoon for three days. Fecal samples were collected on the third day and the diet changed. With the exception of Mertensia and Lathyrus-Vicia, identifiable fragments of forbs (e.g. Heracleum, Potentilla, Thalictrum, Taraxacum, Agoseris, Aquilegia) were rarely or never present in the fecal samples, even when the yearling had eaten only one species for three days. The use of unattached hairs and trichomes to judge the presence or absence of a species results in overestimation (Slater and Jones, 1971; Howard and Samuel, 1979) and in many cases, these structures did not exhibit unique characteristics and were useless in distinguishing species.

Therefore, only qualitative estimates of diet were possible from Marmot Meadow. Other than grasses, cinquefoil and dandelion were the most abundant species in the meadow, and the epidermis

of these forbs evidently does not survive digestion. There is a greater diversity of vegetation at Picnic and quantitative results were obtained from some samples there. However, forbs were no doubt underestimated relative to grasses.

Marmots were observed in the field for more than 500 hours during the summers of 1978-1980. When possible, the species on which the marmots were feeding were recorded.

RESULTS

At both colony sites grass and forb biomass in the spring was low (Fig. 1). Plant growth was rapid thereafter. Plant biomass peaked in mid-season; subsequently, biomass levels dropped precipitously at Picnic and decreased more slowly at Marmot Meadow. A similar increase in biomass was evident through the beginning of August at Marmot Meadow in 1969 (Kilgore and Armitage, 1978).

At Picnic, grasses, Thalictrum, Potentilla, and Epilobium comprised from 57.3 to 82.0% of the total biomass in 1979, and 45.4 to 76.8% in 1980 (Table 1). Other species of forbs each contributed <10% to the total biomass with the exception of Aquilegia in the second sampling period in 1979. Grasses, Potentilla and Taraxacum were the most abundant plants at Marmot Meadow in both years, totalling 79.1 to 91.7% of the biomass in 1979, and 70.8 to 88.3% in 1980 (Table 1). Of the other herbaceous plants, only Mertensia fusiformis (on the first sampling day, 1980) contributed more than 10% of the total biomass. Shrubby vegetation (Potentilla fruticosa and

Arctostaphylos uva-ursi) was sampled twice, and both times comprised less than 10% by weight of all vegetation clipped that day. A flowering Frasera speciosus can weigh more than 200g and an individual Veratrum californicum usually weighs over 30g. In August, Frasera biomass was 34.9% of the total and Veratrum contributed less than 10% to the total biomass. Marmots were never observed to feed on either Frasera or Veratrum.

The nitrogen content of dried plant material is an estimate of protein content. Per cent N was multiplied by 6.25 to convert to crude protein which is expressed as a percentage of the dry weight. Frequently, 75 - 85% of the nitrogen in a plant is protein. The other nitrogenous constituents include inorganic N, free amino acids, peptides of low molecular weight, nucleic acids, and alkaloids (Lyttleton, 1973).

Early summer values of crude protein ranged from 44.7% for Vicia to only 16.3% for Claytonia, an ephemeral, early-blooming plant (Table 2). For most species, crude protein in late summer was approximately one half of what it was early in the season; only Thalictrum maintained the same level of crude protein throughout the summer.

Marmots rarely have been observed to drink in the wild; therefore, external sources of water are confined to dew and the water content of their food. Water content of grasses, sedge, and selected forbs ranged from 60.0 to 83.4% by weight in June (Table 3). Although vegetation at Marmot Meadow appeared to start drying up during the first week in August, not all forbs decreased in water content as the season advanced. Three of six

forbs had an August water content only slightly less than that in June (Table 3).

Virtually all the recognizable epidermal fragments in fecal samples from Marmot Meadow at the end of June were grasses. The pappus of dandelion seeds and Claytonia fragments were present but rare. Few dandelions were blooming at this time and Claytonia was much less than 1% by weight of the vegetation. Two weeks later, grasses were still the most frequent species in the feces, but the number of dandelion pappuses increased greatly and some Mertensia fusiformis was identified. By the third week in July, seed coats appeared in the feces and the Mertensia fragments recorded were probably ciliata. Grass and dandelion pappuses were common. In early August, infrequent fragments of Carex, Thalictrum, and Lathyrus-Vicia were observed in addition to grasses and dandelion. Many seeds were apparent in feces collected the third week of August. Grass was less common than at any other time. Agoseris and Lathyrus-Vicia were the only forbs detected. Marmots were observed to forage heavily on Potentilla and dandelion flowers in Marmot Meadow.

Quantitative estimates of diet composition were made on three samples from Picnic (Table 4). As at Marmot Meadow, consumption of grasses decreased and seed consumption increased as the summer advanced. Claytonia was an important dietary component in June and July, and Lathyrus-Vicia and Heracleum were important in August.

Relationships between plant characteristics and diet choice were unclear. Marmots did not consistently select species in the

high category of any of the factors examined. Calytonia and grasses, both low in crude protein, were eaten extensively. Claytonia, making up only a small percentage of the total vegetation biomass, was certainly a preferred species. The greater consumption of grass at Marmot Meadow was correlated with the greater biomass of grasses at Marmot Meadow (Table 1, Table 4). Dandelion heads were common in the Marmot Meadow diet and ranked high in relative biomass there. At Picnic, dandelion was an insignificant dietary component and ranked low in biomass. These correlations indicate that dandelion was not selected, but eaten in proportion to its abundance.

Vegetation offered to the captive yearlings included the species listed in Table 1 (excluding Delphinium and Claytonia) and Linum lewisi, Ipomopsis aggregata, and Castilleja sulphurea. Epilobium and Linum were not eaten and Achillea was not eaten until several hours had elapsed.

DISCUSSION

Yellow-bellied marmots feed selectively (Armitage, 1979). According to Westoby (1974) the objective of food selection is to obtain the best mix of nutrients within a fixed total intake. For most animals, more than one factor determines the pattern and degree of selectivity. The marmots did not appear to choose their mix of forage species on the basis of any single factor. No one plant species ranked in the high group for all the factors considered in this study.

The best diet for a herbivore may not be the one which maximizes caloric intake (Pulliam, 1974), although if energy intake is limiting, an animal will selectively consume the parts of plants that are highest in calories (kudus, Owen-Smith and Novellie, 1982). Gray squirrels chose food items that maximized energy intake regardless of the concentration of preferred food (Lewis, 1980). Heteromyid rodents on the other hand, did not choose only high energy seeds, suggesting that other nutritional needs influenced selection (Reichman, 1977).

Protein may be in short supply for a herbivore due to the relatively low levels of protein that commonly occur in most plants. Protein content affects forage choice in many mammals (e.g. rabbits and hares, Miller, 1968; gazelles, Bell, 1970; howler monkeys, Milton, 1979). However, animals do not necessarily choose those plants which contain the most protein. Grouse preferred heather with a high nitrogen content only in winter (Miller, 1968). Beach voles chose the parts of beach grass highest in protein only in the spring and summer (Goldberg et al. 1980). Such a pattern of seasonal change indicates that either protein is not limiting at all times of the year or that additional factors influence selection.

Grasses do not usually contain chemical anti-herbivore defenses (McNaughton, 1979) and on that basis, should be readily eaten by marmots. The seasonal decrease in the use of grass as forage by the marmots might be related to the decrease in crude protein content (and/or water) as the summer progressed. Poa alpina decreases in digestibility as it matures (Johnston et al.,

1968). The increased importance of seeds in the diet late in the summer might be related to protein needs as well as the increase in seed abundance at both sites. Seeds are high in protein (Mattson, 1980) and eating them would allow the marmot to compensate for the concomitant crude protein decrease in leafy vegetation. Seeds also represent a relatively concentrated source of energy (Brown et al., 1979), and it is not surprising that marmots take advantage of this seasonally abundant resource.

For some animals, the water content of forage is an important source of moisture. A high water content is often associated with high digestibility and high nutrient concentration. The water content in alpine plants was significantly correlated with palatability in feeding trials with Spermophilus parryii (Batzli and Sobaski, 1980). Heracleum was the preferred plant of marmots in feeding trials (Armitage, 1979). Its high water content (Table 3) might explain the marmots' preference for it.

Regardless of the benefits of including any one species in the diet, relative abundance of that plant will affect the frequency with which it appears in the diet. Obviously, even if a plant is greatly preferred, if it is not abundant, it cannot be a major component of the diet. Marmots responded in part to relative abundance. Dandelion, and probably other species that were uncommon and not highly preferred (e.g. Carex), were eaten in proportion to their abundance. Although toxicity of the forage was not examined, prairie dogs (Cynomys ludovicianus) switched their feeding preference in response to changes in relative abundance of potential food resources (King, 1955).

Maiorana (1978) proposed that food choice may, in fact, reflect species availability, and that if a common plant contains toxic compounds, a herbivore may evolve a mechanism to deal with it and thus exploit an abundant resource.

Plant secondary compounds play a role in determining the pattern of selectivity (Freeland and Janzen, 1974). For example, alkaloid levels were negatively correlated with the palatability of grass leaves to meadow voles (Kendall and Sherwood, 1975) and tannins reduced the palatability of leaves to colobus monkeys (Oates et al., 1977).

Secondary compounds did reduce palatability, and caged marmots in this and Armitage's study (1979) rejected alkaloid-containing Aquilegia, Delphinium, and Achillea (Raffauf, 1970); the presence of oxalate (T. Foppe, pers. comm.) was probably responsible for the rejection of Epilobium. Hoary marmots in Alaska also did not eat Epilobium, even though abundant (Hansen, 1975). Linum may be unpalatable to Colorado yellow-bellied marmots because of toxic compounds, but data are lacking. Some alkaloid-bearing plants were eaten, however, (Lathyrus, Thalictrum; Raffauf, 1970), indicating that some alkaloids can be tolerated in the diet. Jung (1977) hypothesized that a herbivore ingests increasing amounts of a toxic plant as the nutritional value of that plant increases relative to other available forage. This hypothesis may partially explain the pattern of increased consumption of Lathyrus or Vicia in late summer when Claytonia was no longer available and the forage value of grasses had decreased.

A host of additional properties of a plant (sodium, potassium, and lignin content) can affect an animal's choice of forage. Herbivores such as marmots evidently choose their food on the basis of several factors. Rejection of a plant was due to potential toxicity; some species were eaten in roughly the same proportion as they occurred in the feeding areas and others were definitely preferred. Unfortunately, the inability to quantify the marmot diet precluded determining which nutritional variables were responsible for the marmots' selection. Westoby (1974) suggested a linear programming model to construct the optimal diet. Any number of nutrients (defined by Westoby as any property of the food that affects the animals' welfare) can be included in his model, but the researcher must have an a priori knowledge of the optimal amount of each nutrient. If dietary composition could be accurately determined, and data obtained on several nutritional properties of plants in the diet, a multivariate analysis might elucidate which of the nutrient factors are most important to the animal at different times of the year.

ACKNOWLEDGMENTS

This work is part of a dissertation submitted by B. Frase in partial fulfillment of the requirements for the Ph.D. degree at the University of Kansas. Field research was funded by NSF Grants DEB 78-07327 and DEB 81-212331 and was conducted at the Rocky Mountain Biological Laboratory in Colorado. We thank R. S. Hoffmann and R. Jander for critically reading the manuscript. We are grateful to G. Seimuir of the Mountain Meadow Research Station, Gunnison, Colorado, for the use of a Wiley mill. We would like to thank T. Foppe and R. Hansen of Colorado State University for advice concerning fecal analysis techniques, and Kevin and Keith Armitage for assistance in the field.

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Table 1. Per cent of total biomass (dry weight). Sampling periods are approximately two weeks apart, beginning in the third week of June. '79 and '80 represent the years in which plants were collected.

<u>Species</u>	<u>Sampling Period</u>											
	<u>I</u>		<u>II</u>		<u>III</u>		<u>IV</u>		<u>V</u>		<u>VI</u>	
	'79	'80	'79	'80	'79	'80	'79	'80	'79	'80	'79	'80
Marmot Meadow												
<u>Potentilla gracilis</u>	38.6	39.9	24.0	48.3	52.8	49.7	57.7	45.2	58.0	46.4	33.9	
Grasses	32.9	25.7	36.2	19.0	24.9	26.5	21.5	33.5	26.5	31.8	40.7	
<u>Taraxacum officinale</u>	7.8	5.2	18.9	13.9	8.5	7.5	7.5	9.6	3.4	2.6	11.0	
<u>Lathyrus leucanthus</u>	3.1	5.6	1.6	8.5	4.1	2.8	5.8	3.1	2.1	9.2	3.8	
<u>Mertensia fusiformis</u>	5.0	14.4	3.2	2.8	1.1	1.0	-	-	-	-	-	
<u>Thalictrum fendleri</u>	1.7	1.0	0.3	0.2	1.1	-	-	1.6	-	-	-	
<u>Vicia americana</u>	-	3.0	-	0.4	0.4	1.3	0.7	0.6	-	0.5	0.9	
<u>Achillea millefolium</u>	-	-	-	1.7	-	3.3	-	2.7	*	3.7	-	
<u>Agoseris glauca</u>	-	-	*	-	*	6.1	*	2.3	-	1.9	-	
Other	10.8	4.9	15.9	5.3	7.7	1.5	6.9	1.5	10.0	3.7	9.7	

Table 1. continued.

<u>Species</u>	<u>I</u>		<u>II</u>		<u>III</u>		<u>IV</u>		<u>V</u>	<u>VI</u>
	'79	'80	'79	'80	'79	'80	'79	'80	'79	'79
Picnic	22.0	10.5	17.2	10.9	28.7	17.6	7.7	16.6	11.4	36.8
<u>Potentilla gracilis</u>										
Grasses	15.4	14.2	12.7	8.4	4.2	14.6	10.3	10.5	12.2	11.3
<u>Thalictrum fendleri</u>	23.2	25.4	19.4	14.1	12.5	13.5	19.0	24.8	16.4	11.0
<u>Epilobium angustifolium</u>	5.1		*	12.0	21.5	30.4	20.3	24.9	42.0	9.8
<u>Aquilegia caerulea</u>	6.7	3.3	17.2	7.0	6.0	5.7	6.5	0.5	5.9	-
<u>Lathyrus leucanthus</u>	0.5	1.8	1.2	1.1	2.7	0.7	1.5	3.0	1.4	4.3
<u>Vicia americana</u>	1.4	1.0	-	0.1	1.0	0.1	2.4	-	-	0.1
<u>Taraxacum officinale</u>	0.2	-	0.1	-	1.0	-	0.1	-	0.1	0.1
<u>Mertensia fusiformis</u>	1.9	-	-	-	-	-	-	-	-	-
<u>Delphinium barbeyi</u>		2.0		2.0	1.9	7.2	6.6	-	2.3	2.8
<u>Heracleum lanatum</u>	-	-	-	0.2	4.7	-	-	-	-	-
<u>Mertensia ciliata</u>	-	-	-	1.2	-	-	2.8	-	-	-
<u>Claytonia lanceolata</u>	*	2.6	*	-	-	-	*	-	-	-
<u>Achillea millifolium</u>		0.2		0.6	*	0.5	*	0.3		
Other	23.7	40.2	32.2	42.5	17.5	9.8	25.0	19.4	10.4	23.5

included in Other. Other includes species that were rare and not known to be eaten by marmots.

- not present in any clipped quadrat or weighing less than 1 g.

Table 2. Crude protein content of green leaves and stems of plants present in the colony sites. H = high protein group, M = medium protein group, L = low protein group. represents value that does not differ from previous measure by more than $\pm 0.3\%$ N, the accuracy limits of the Coleman Nitrogen Analyzer.

<u>Species</u>	<u>23-24 June</u>	<u>6-13 July</u>	<u>21-30 July</u>	<u>7-12 August</u>	<u>21 August</u>
<u>Vicia americana</u>	44.78 H		27.13 H	20.81 H	19.00 H
<u>Delphinium barbeyi</u>	33.81 H	25.75 M	20.81 M		
<u>Mertensia fusiformis</u>	31.69 H	15.63 L	15.60 L*		
<u>Potentilla gracilis</u>	27.50 M	20.50 M	17.38 L	16.19 M	16.88 H
<u>Achillea millifolium</u>	29.06 M	21.88 M	19.44 M	16.00 M	14.56 M
<u>Aquilegia caerulea</u>	26.19 M		16.19 L		
<u>Lathyrus leucanthus</u>	23.19 M	28.44 H	20.38 M	16.19 M	12.81 L
<u>Taraxacum officinale</u>	26.19 M	20.75 M	16.69 L	20.38 H	15.31 M
Grasses	25.06 M	19.63 L	17.00 L	10.38 L	11.44 L*
<u>Thalictrum fendleri</u>	21.81 L	18.19 L	22.00 M	23.25 H*	
<u>Claytonia lanceolata</u>	16.31 L				
<u>Agoseris glauca</u>			22.12 M	17.75 M	13.25 L
<u>Epilobium augustifolium</u>		25.06 M	15.00 L		
<u>Heracleum lanatum</u>		29.81 H		16.88 M	

Table 3. Water content expressed as per cent of dry weight.

Plants collected in Marmot Meadow. June data from
Kilgore (pers. comm.)

<u>High water content</u>	<u>June</u>	<u>August</u>
Grasses	85.7	
<u>Taraxacum officinale</u>	83.4	80.2
<u>Heracleum lanatum</u>		82.4
<u>Mertensia ciliata</u>		80.8
<u>Medium water content</u>		
<u>Agoseris glauca</u>	77.5	72.5
<u>Lathyrus leucanthus</u>	75.8	66.6
<u>Low water content</u>		
<u>Vicia americana</u>	71.9	69.1
<u>Thalictrum fendleri</u>	70.5	62.7
<u>Achillea millefolium</u>	69.2	
<u>Potentilla gracilis</u>	68.5	68.6
<u>Mertensia fusiformis</u>	60.0	



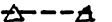

Table 4. Diet composition of yellow-bellied marmots living at
Picnic, 1980.

	<u>24 June</u>	<u>13 July</u>	<u>12 August</u>
Grasses	67.80	41.70	16.08
<u>Claytonia lanceolata</u>	28.54	23.25	
<u>Lathyrus-Vicia</u>	1.83	4.80	41.32
<u>Mertensia fusiformis</u>	1.83		
<u>Potentilla gracilis</u>		13.09	
Seeds		10.15	23.03
<u>Agoseris glauca</u>		2.34	
<u>Delphinium barbeyi</u>		2.34	
<u>Mertensia ciliata</u>		2.34	
<u>Heracleum lanatum</u>			10.06
<u>Carex</u> sp.			4.75
<u>Achillea millefolium</u>			4.75

Table 5. Caloric content of dried plant tissues. Caloric values are cal g⁻¹ ash-free dry weight. Data are from Kilgore (1972).

<u>High calorie group</u>	<u>Caloric content</u>
<u>Vicia americana</u>	5398
<u>Thalictrum fendleri</u>	5354
<u>Laythrus leucanthus</u>	5346
<u>Carex egglestonii</u>	5189
 <u>Medium calorie group</u>	
<u>Fragaria ovalis</u>	5004
<u>Grasses</u>	4995
<u>Mertensia ciliata</u>	4918
<u>Achillea millefolium</u>	4877
 <u>Low calorie group</u>	
<u>Agoseris glauca</u>	4861
<u>Taraxacum officinale</u>	4728
<u>Potentilla gracilis</u>	4712

FIGURE LEGEND

Figure 1. Biomass estimates from clipped quadrats. Sampling occurred at approximately two week intervals, beginning 23 June and ending 11 September.  Marmot Meadow, 1979;  Marmot Meadow 1980;  Picnic 1979;  Picnic, 1980.

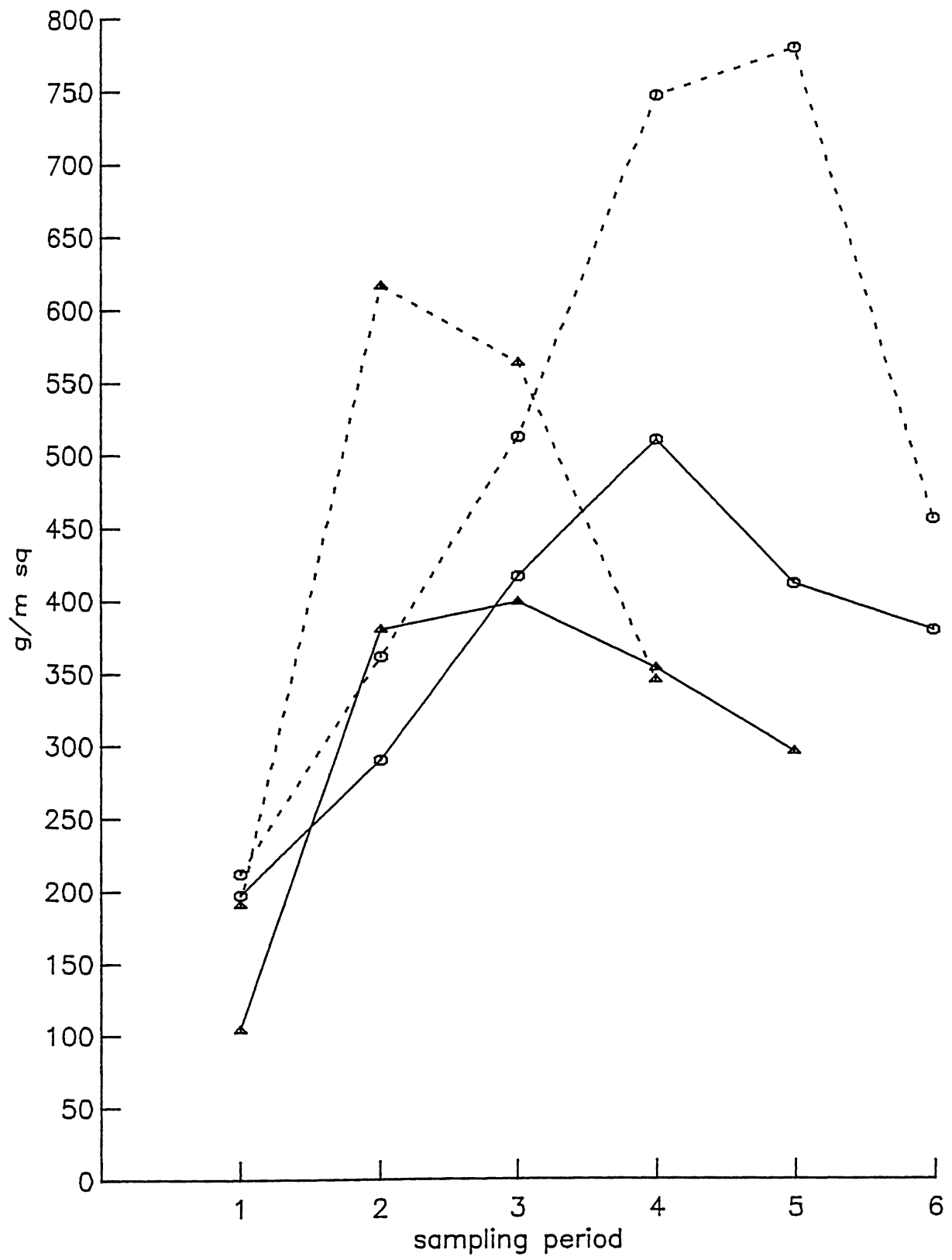


Figure 1. Biomass based on clipped quadrats